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Article (Published Version)

Griffiths-Lee, Janine, Nicholls, Elizabeth and Goulson, Dave (2020) Companion planting to attract pollinators increases the yield and quality of strawberry fruit in gardens and allotments. *Ecological Entomology*. ISSN 0307-6946

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Companion planting to attract pollinators increases the yield and quality of strawberry fruit in gardens and allotments

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Abstract. 1. Global pollinator declines have led to concern that crop yields might fall as a result of a pollination deficit. Companion planting is a traditional practice thought to increase yield of insect pollinated crops by planting a co-flowering species next to the crop.

2. Using a combination of conventional researcher-led experiments and observational citizen scientist data, we tested the effectiveness of bee-friendly borage (*Borago officinalis*) as a companion plant to strawberry (*Fragaria x ananassa*). Insect visitors to the 'Test' (strawberry + borage) versus 'Control' (strawberry only) plants were observed, and strawberry fruit collected. Strawberries collected during the researcher-led experiment were also subject to fruit measurements and assessments of market quality.

3. Companion plants were found to significantly increase both yield and market quality of strawberries, suggesting an increase in insect pollination per plant. Test strawberries companion planted with borage produced an average of 35% more fruits, and 32% increased yield by weight. Test strawberry plants produced significantly more fruit of higher aesthetic quality when assessed by Marketing Standards for Strawberries.

4. Although there was no significant difference in the overall insect visits, when broken down by broad insect group there were significantly more flies visiting the test strawberries than controls.

5. These results could have implications for both gardeners and commercial growers. As consumers prefer a cosmetically perfect fruit, the production of fruit with increased aesthetics aids food waste reduction.

Key words. Borage, citizen science, companion plant, fruit set, pollinator, strawberry.

Introduction

Over one-third of global food production is generated by crops that benefit from animal pollination (Klein et al., 2007). Yet this vital ecosystem service is threatened by a suite of anthropogenic factors, including habitat loss, pesticide use, disease, climate change, and invasive species (Potts et al., 2010; Vanbergen, & Initiative, the I. P., 2013; Goulson, Nicholls, Botias, & Rotheray, 2015; Powney et al., 2019).

Pollinator declines have led to a growth in the trade of managed honeybees, bumblebees, and some solitary bees, which are redistributed around the world to enhance crop pollination (Goulson, 2003). An estimated 15 000 bumblebee nests

are purchased for use in soft fruit farms per annum in the U.K. (Goulson, 2010). However, this commercialisation poses risks for wild bee populations, including the transmission of pathogens and parasites (Colla, Otterstatter, Gegeer, & Thomson, 2006; Graystock et al., 2013; Schmid-Hempel et al., 2014) and competition for floral resources and nesting sites (Ings, Ward, & Chittka, 2006; Inoue, Yokoyama, & Washitani, 2008).

An alternative to introducing managed bees to aid pollination is to support the existing wild pollinator population through planting of additional floral resources. Much research is currently focused on encouraging a diverse array of pollinators to agricultural environments using wildflowers (Carreck & Williams, 2002; Carvell, Meek, Pywell, Goulson, & Nowakowski, 2006; Blaauw & Isaacs, 2014; Woodcock et al., 2014; Pywell et al., 2015). Considering strawberry plants in particular, pollinator visits have been estimated 25% higher

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when adjacent to wildflower strips (Feltham, Park, Minderman, & Goulson, 2015). Enhancement of existing ecosystem services through ‘ecological intensification’ can also improve the yields of small-scale farmers (Garibaldi et al., 2016). With urban agriculture frequently occurring in community gardens and allotments (Mougeot, 1999) such ‘ecological intensification’ (Garibaldi et al., 2016) could also be beneficial in improving the yields of crop plants grown in urban community gardens and allotments. This is of considerable significance given that globally, 800 million people practise urban agriculture (FAO, 2019).

Companion planting is a traditional gardening practice whereby a second flowering plant species is deliberately planted alongside a crop with the ultimate aim of improving yield (Franck, 1983). Companion planting of ‘banker’ plants is well researched in the context of encouraging natural predators of crop pests (Frank, 2010; Sigsgaard et al., 2013; Balzan, 2017). Planting of co-flowering species can also improve pollination services through pollination facilitation (Lavery, 1992; Feldman, Morris, & Wilson, 2004; Ghazoul, 2006). However, a recent study on intercropping strawberries in a commercial setting concluded limited evidence of enhanced pollination services (Hodgkiss, Brown, & Fountain, 2019). Indeed studies have shown that more attractive plant species can distract pollinators from a particular focal plant (Chittka & Schürkens, 2001; Diekötter, Kadoya, Peter, Wolters, & Jauker, 2010; Foulis & Goulson, 2014; Nicholson et al., 2019).

The cultivated strawberry (*Fragaria x ananassa* Duch.) is a member of the family Rosaceae. Strawberries are a popular commercial fruit, with U.K. production in 2017 over 127 600 tonnes (FAOSTAT, 2019) and they are also widely grown in allotments and gardens all over the U.K. The achenes of the strawberry are the true fruits, each containing an ovule that when fertilised produce the hormone auxin (Nitsch, 1950). Auxin stimulates growth of the receptacle, so for a perfectly shaped fleshy ‘strawberry’ most of the ovules must be fertilised, if too few are fertilised an irregular shaped ‘nubbin’ will result (McGregor, 1976). Self-pollination of strawberry flowers is possible, although as the stigmas of the strawberry flower are receptive before the anthers dehisce and pollen is available, cross pollination is more effective (McGregor, 1976).

Cross pollination in strawberries can result in increased yield and market quality (e.g. Bartomeus et al., 2014; Klatt et al., 2014a). Early studies concluded that insects are more effective pollinators than wind in the pollination of strawberry flowers (Kronenberg, 1959; Hughes, 1961). Furthermore, Connor and Martin (1973) estimated that self-pollination can account for the development of 53% of the achenes, with wind motion increased this to 67%, and insect pollination increased it further to 91%. Recent estimates of UK strawberry yield attribute 45% to pollinators (Smith et al., 2011), while Wietzke et al. (2018) report a 92% increase in the commercial value of marketable strawberry fruits in the presence of insect pollinators. Other studies having reported decreased malformations in strawberry fruit pollinated by insects (Klatt, Klaus, Westphal, & Tschardt, 2014b; Abrol, Gorka, Ansari, Al-Ghamdi, & Al-Kahtani, 2019; Herrmann, Beye, de la Broise, Hartlep, & Diekötter, 2019).

In this study, we examined the potential benefits of companion planting strawberry with borage (*Borago officinalis*). Borage is an annual herb from the family Boraginaceae. A common garden plant, borage is very attractive to pollinators (Carreck & Williams, 2002; Garbuzov & Ratnieks, 2014; Rollings & Goulson, 2019), and frequently features in gardening lists of bee-friendly plants (e.g. The Wildlife Trusts, 2019). This study was conducted in two parts: by professional scientists on the campus of the University of Sussex, U.K., and by volunteer ‘citizen scientists’ at various locations across the U.K. Citizen science has been used for a range of disciplines and monitoring at a range of levels – from species to ecosystems (Dickinson et al., 2012). Citizen science projects have become popular, gathering data that would otherwise require massive resources while engaging the public in scientific research, and they are increasingly supported by new technologies (Pocock, Chapman, Sheppard, & Roy, 2013). Many citizen science projects have focused on pollinators (Phillips, 2008; Deguines, Julliard, de Flores, & Fontaine, 2012; Lye, Osborne, Park, & Goulson, 2012; Oberhauser & LeBuhn, 2012; Birkin & Goulson, 2015; Roy, Baxter, Saunders, & Pocock, 2016) contributing valuable scientific data to the field.

The aims of the experiment were fourfold: to test whether the presence of a companion plant (i) increases insect visitations to a crop (ii) increases the yield of a crop (iii) increases the quality of the fruit, and also, (iv) to compare the experimental results found by volunteers when compared to professional scientists. Aim (iv) serves to gauge the feasibility and reliability of such experimental pollinator experiments being conducted by citizen scientists.

Materials and methods

Study plants

Everbearing strawberry plants (*Fragaria x ananassa*) ‘Albion’ variety (Ken Muir Ltd, Essex, U.K.) produce flowers from April to August; thus, were selected to maximise the likelihood of an overlap in flowering between borage and strawberry plants over a geographically large area (see supplementary Data S1 for locations of citizen scientists around the U.K.). Albion variety is a disease resistant, hardy plant, ideal for growth in containers (Ashbridge Nurseries, 2018), and readily available to purchase in garden centres. Although the seed-like achenes are the true fruits, in this paper we will refer to the entire fleshy receptacle of the strawberry as an individual ‘fruit’. Borage blue (*Borago officinalis*) (Sarah Raven’s Kitchen and Garden Ltd, Marlborough, U.K.) was selected as the companion plant. It is an annual with a long flowering period, that is highly attractive to pollinators, hardy, easy to germinate from seed, and suitable for growing in containers.

Researcher experiment

Researcher-led experiments took place on the University of Sussex campus, Brighton, U.K., between March and August 2018. Strawberry runners were planted individually in 6 litre

'Hadopot™' containers (Hadopots Ltd, Malvern, U.K.; hereafter 'pot') with organic compost, and kept in an unheated greenhouse. Any strawberry runners or flowers were removed to conserve the plants' energy until the experiment started. Three borage seeds were planted in a 13.5 litre pot and kept in the greenhouse, initially under UV light for 2 weeks. After initial growth, plants were thinned to the two strongest borage seedlings per pot.

Once the strawberry plants and borage were flowering simultaneously, they were placed in 26 different sites around the campus, a minimum of 30 m apart. One pot containing a single strawberry plant ('Test') was placed directly next to a borage plant and one pot containing a single strawberry plant ('Control') was placed three metres away from the Test strawberry plant and borage in a paired design. Both Test and Control plants were kept at least three metres from all other flowering plants. This distance was constrained by the fact that citizen scientists would be conducting the experiment in their gardens and allotments and therefore would be limited on space. All three-plant pots (Control, Test, Borage) were placed in the same aspect and labelled with a unique ID.

Pollinator observations

Over a period of 4 weeks during June and July 2018, insect visits to the flowering strawberry and borage plants were observed weekly. Insects were categorised as one of the following broad taxonomic groups: beetle, hoverfly, 'other fly', butterfly/moth, bumblebee, honeybee, solitary bee, wasp, and 'other' insects. Visits were recorded for 5 min per plant (Control strawberry, Test strawberry, and Borage), between 10 AM and 4 PM, on sunny, low-wind days when temperatures were above 13 °C. If the strawberry plant did not have any flowers, visits were not recorded. If the Test strawberry did not have flowers, visits to the borage plant were also not recorded. The number of open flowers on the strawberry plants was recorded during the weekly insect visits; as the flowers last less than 3 days (personal observation), it was assumed that flowers were not counted twice.

Strawberry fruit harvest

After the end of the 4-week pollination period, the strawberry plants were brought back into the greenhouse so the strawberry fruit could ripen in conditions with a reduced threat of pests, and to facilitate fruit harvesting. At this point, a permanent marker (Sharpie, Sanford L.P) was used to make a red mark on the stems of all flowers, nubbins, unripe, and ripe fruit. From this point onwards, any newly opening flowers or fruit developing from unmarked stems were removed and disposed of, ensuring that only fruit resulting from flowers pollinated in the field were harvested. Strawberries were harvested when deep red in colour.

Strawberry quality and fruit measurements

Strawberry fruit diameter and length in millimetres was first recorded using digital callipers. Fresh weight was then recorded

to the nearest hundredth of a gram (Precisa 125A, Precisa Gravimetrics AG, Switzerland). The quality of individual strawberries was assessed according to the Marketing Standards for Strawberries (Rural Payments Agency, 2011). The assessment standards were as follows: EXTRA class = bright red, defect free, 25 mm + diameter; Class I = white patch of <10%, slight defects, 18 mm +, slight pressure marks; Class II = white patch <20%, defects, 18 mm +, slight bruising; N/A = damaged, not intact, deteriorating, foreign matter, pests, damage, external moisture, or foreign smell/taste. Assessment was conducted blind to the experimental treatment, to eliminate any bias.

A refractometer (0–50%) was used measure the sugar content of strawberry juice (Degrees Brix, % sugar content of aqueous solution). Half of each strawberry was placed in an oven at 40 °C for 7 days to fully dehydrate the fruit and calculate the water content (dry weight subtracted from wet weight divided by two). The second half of the fruit was macerated using a kitchen hand blender (Bosch BSH home appliances ltd, Milton Keynes, U.K.), along with 200 ml of water, following the protocol detailed in Hodgkiss, Brown, & Fountain (2018). The mixture was allowed to settle for 20 min, and then sunken fertilised achenes and floating unfertilised achenes were counted.

Citizen scientist project packs and methodology

One hundred and ten volunteers were recruited at various locations around the U.K. (Data S1). Volunteer citizen scientists who had previously taken part in similar projects run by The University of Sussex were invited to participate in the 'Super Strawberries' project, which was also advertised via Twitter. Volunteers were sent a pack including two dormant 'Albion' variety strawberry runners, one pack of borage seeds, two 6 litre pots, one 13.5 litre pot, and a workbook (see supplementary Data S2, S3, and S4 for workbook, instructions, and ID guide). A full list of pack contents is available in S3. The protocol followed by the volunteers was the same as the researcher experiment, with the exception of the laboratory-based strawberry measurements. Instead, volunteers were asked to count and weigh the harvested red fruits weekly.

Data analysis

Data analysis was carried out in R version 3.5 (R Core Team, 2018). All data submitted by citizen scientists on insect visits and harvest were used in analysis, although the data differed in terms of completion. Fruit quality and measurement data were available for the researcher experiment only.

Pollinator observations. To test for differences in insect visitation and the number of flowers produced by strawberry plants that were either paired (Test) or not paired (Control) with the companion plant, a Generalised Linear Mixed Model (GLMM) with Poisson distribution was used, with plant treatment (Test vs. Control) as a fixed effect, experimental week as a random effect and site and individual plant ID as nested random effects. Total insect visits were analysed both separately for the citizen

scientist and researcher data set, and also in combination. For analysis of the insect visitations by separate taxonomic groups (beetle, hoverfly, 'other fly', butterfly/moth, bumblebee, honeybee, solitary bee, wasp, and 'other' insects), the combined data set was used, as the counts of insects for certain groups were too low for the data to be split by experiment.

Fruit harvest. To compare yields by fruit number between strawberry plants that were paired (Test) or not (Control) with the companion plant, a GLMM with Poisson distribution was used to test for differences in the number of strawberry fruits produced per plant. Plant treatment (Test/Control) was a fixed effect and site was a random effect. The citizen scientist and researcher data sets were analysed separately and in combination. To compare the yield by fruit weight between strawberry plants that were paired (Test) or not (Control) with the companion plant, a Linear Mixed Model (LMM) was used to test differences between the total fruit fresh weight produced per plant. Plant treatment (Test/Control) was a fixed effect and site was a random effect. The citizen scientist and researcher data sets were analysed separately and in combination, although any obvious erroneous strawberry weight entries from citizen scientists were omitted from analysis.

Fruit quality and measurements. LMMs were used to compare fruit measurements: fruit diameter, length, fresh weight, Brix, water content, and proportion of fertilised achenes. For all fruit measurements, plant treatment (Test/Control) was a fixed effect and site and plant ID as nested random effects. The proportion of fruit in each market class was compared between treatment groups using a χ^2 test.

Results

Pollinator observations

Considering the combined data set that includes both the researcher and citizen science experiments, the number of flowers did not differ significantly between the test and control plants (GLMM: $X^2 = 0.456$, $df = 1$, $P = 0.499$) (Test, mean \pm SE: 7.36 ± 0.297 and Control, mean \pm SE: 7.0 ± 0.349), so the number of flowers was not included in further analysis of insect visitation. There was no significant difference between the mean number of total insect visitors between treatments (Test, mean \pm SE: 1.60 ± 0.161 and Control, mean \pm SE: 1.35 ± 0.138) (Fig. 1; GLMM: $X^2 = 0.409$, $df = 1$, $P = 0.523$).

The citizen scientist and researcher experiments were then analysed individually in terms of differences in total insect visitations between strawberry treatments. Firstly for the researcher experiment, the mean number of insect visitors did not significantly differ between the test strawberry plant paired with borage and the control plant (GLMM: $X^2 = 0.152$, $df = 1$, $P = 0.697$) (Test, mean \pm SE: 1.22 ± 0.215 and Control, mean \pm SE: 1.31 ± 0.18). There was also no statistically significant difference in the mean number of insect visitors between the test and control plants for the citizen scientist experiment

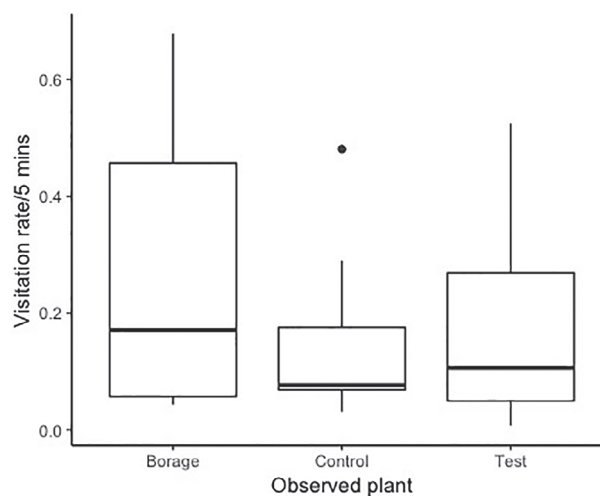


Fig. 1. Overall insect visits (by visitation rate – mean per five-minute observations), to test strawberry, control strawberry, and borage plants. Showing the median (central horizontal lines). As the number of 5-min observations for each treatment differed, an overall mean visitation rate per plant was calculated [by dividing the insect group total count by the total number of 5-min observations for each plant treatment (borage $n = 140$, control $n = 131$, test $n = 141$)].

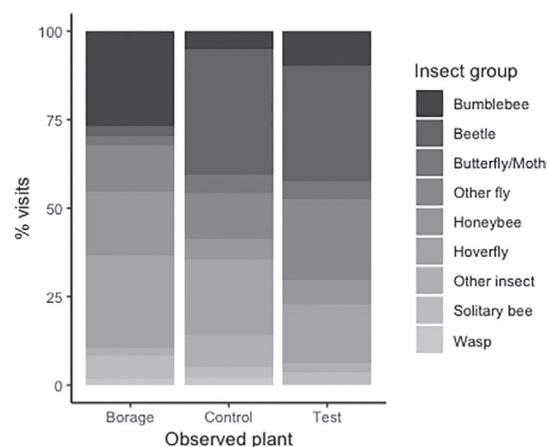


Fig. 2. Percentage insect visits by broad taxonomic group to test strawberry, control strawberry and borage.

(GLMM: $X^2 = 1.547$, $df = 1$, $P = 0.214$) (Test, mean \pm SE: 2.03 ± 0.234 and Control, mean \pm SE: 1.39 ± 0.211).

When insect visits were compared by taxonomic group (Fig. 2), significantly more 'other flies' (excluding hoverflies) visited test strawberry plants paired with borage, compared to the unpaired control plant (Table 1; Test, mean \pm SE: 0.369 ± 0.124 and Control, mean \pm SE: 0.176 ± 0.102), with strawberry plants next to borage receiving more than twice as many visits as plants that were three metres away. Visits to the test and control plants did not differ significantly for other taxonomic groups (Table 1). Although not quite statistically significant, there were also more than twice as many bumblebee visits to strawberry plants adjacent to the companion plant

Table 1. Effect of strawberry plant proximity to the companion plant borage (Test = paired, Control = 3 metres away) on insect visitation, by broad taxonomic group

Insect group	X ²	df	P	Control		Test	
				Mean	SE (±)	Mean	SE (±)
Bumblebee	3.612	1	0.057	0.069	0.111	0.156	0.096
Beetle	0.222	1	0.638	0.481	0.169	0.525	0.185
Butterfly/Moth	0.076	1	0.783	0.069	0.094	0.078	0.102
Other fly*	4.005	1	*0.045	0.176	0.102	0.369	0.124
Honeybee	0.001	1	0.970	0.076	0.093	0.106	0.130
Hoverfly	0.007	1	0.932	0.290	0.118	0.270	0.101
Other insect	1.555	1	0.212	0.122	0.135	0.043	0.096
Solitary bee	0.028	1	0.867	0.038	0.086	0.050	0.094
Wasp	2.212	1	0.137	0.031	0.086	0.007	0.084

* Statistical significance at $P < 0.05$.

(Table 1; Test, mean \pm SE: 0.156 ± 0.096) compared to those placed three metres away (Control, mean \pm SE: 0.069 ± 0.111).

Strawberry fruit harvest

Analysis of harvest by number of fruits using the combined data set indicates that the test strawberry plants placed adjacent to the companion plant produced significantly more fruits than control plants (GLMM: $X^2 = 15.009$, $df = 1$, $P = 0.0001$) (Test, mean \pm SE: 11.3 ± 0.384 and Control, mean \pm SE: 8.36 ± 0.332), with 35% more fruit produced on average, by test plants. This pattern is consistent when the citizen scientist and researcher experiments were considered individually (Fig. 3). For the citizen scientist experiment, the test plant produced significantly more fruit than the control plant (GLMM: $X^2 = 5.55$, $df = 1$, $P = 0.018$) (Test, mean \pm SE: 9 ± 0.734 and Control, mean \pm SE: 6.38 ± 0.573), equating to a 41% increase in the average number of fruit produced. Considering the researcher experiment, the test plant produced significantly more fruit than the control plant (GLMM: $X^2 = 8.859$, $df = 1$, $P = 0.003$) (Test, mean \pm SE: 13 ± 0.408 and Control, mean \pm SE: 10.2 ± 0.373), a 28% increase in the average number of fruit produced.

Analysis of harvest by total weight of fruits using the combined data set indicates that the test strawberry plants placed adjacent to the companion plant produced a significantly higher yield by weight than the control plant, Fig. 4 (LMM: $X^2 = 5.590$, $df = 1$, $P = 0.0181$) (Test, mean \pm SE: 81.688 ± 9.711 and Control, mean \pm SE: 61.91 ± 7.483), with 32% more strawberry yield by weight produced on average, by test plants. Considering only the researcher experiment, the average yield by weight produced by the test plants was 26% higher than the control plants. However, the difference in the total average weight of fruit produced of test plants compared to control plants was not quite statistically significant (LMM: $X^2 = 3.630$, $df = 1$, $P = 0.057$) (Test, mean \pm SE: 85.065 ± 10.627 and Control mean \pm SE: 67.719 ± 8.340). Considering the citizen scientist experiment, the average yield by weight produced by the test plants was 40% higher than the control plants. However, the difference in the total average weight of fruit produced by test plants compared to control plants was also not statistically significant (LMM: $X^2 = 2.029$, $df = 1$,

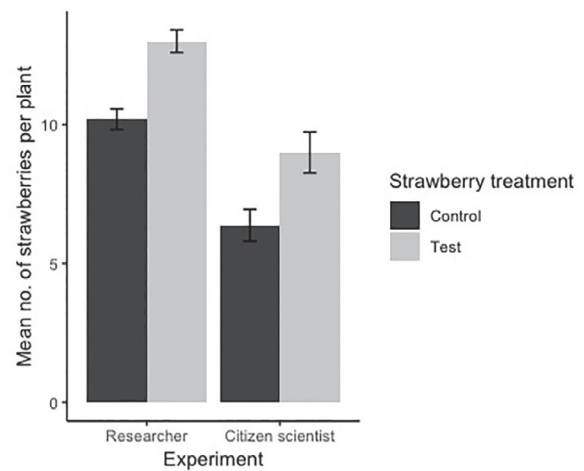


Fig. 3. Mean (\pm SE) number of strawberries produced by test strawberry plants paired with borage compared with unpaired control, for both the citizen science and researcher-led experiments.

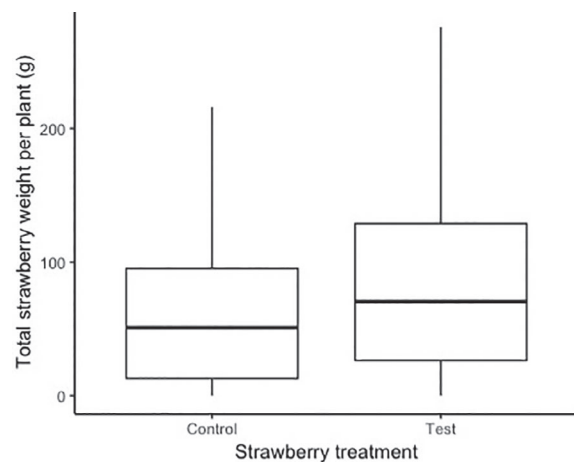


Fig. 4. Total strawberry yield by weight produced per plant, for test plants paired with borage, compared to unpaired control. Showing the median (central horizontal lines).

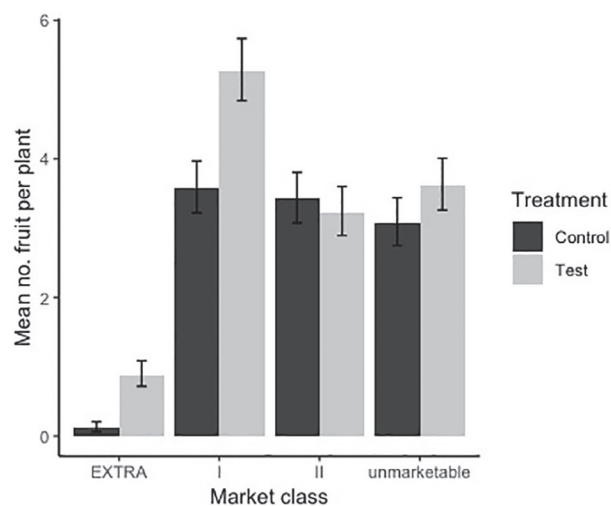


Fig. 5. Mean (\pm SE) number of strawberries classified by Market Class (EXTRA class, Class I, Class II and unmarketable fruit) produced by test strawberry plants paired with borage, compared with unpaired control.

$P = 0.154$) (Test, mean \pm SE: 77.067 ± 18.146 and Control, mean \pm SE: 55.045 ± 13.094).

Strawberry quality and fruit measurements

The categories of market class fruit differed significantly between the test strawberry plants and the control ($X^2 = 16.5$, $P = 0.001$), with more EXTRA class and Class I fruit produced by test strawberry plants than controls (EXTRA test mean \pm SE: 0.885 ± 0.325 fruits, control mean \pm SE: 0.115 ± 0.188 fruits; Class I test mean \pm SE: 5.27 ± 0.39 fruits, control mean \pm SE: 3.58 ± 0.323 fruits), Fig. 5. Comparing fruits harvested from test and control plants, on average there was no significant difference in the fruit measurements (Table 2).

Citizen scientists

One hundred and ten citizen scientists were recruited for the project. Forty-two volunteers (38%) signed up using their allotment, and 68 (62%) using their garden. Sixty volunteers (55%) remained engaged throughout the project (including those that told us when and why they dropped out), with 30 volunteers

(27%) submitting data forms. Of those volunteers who dropped out yet were still engaged, 11 (37%) cited personal reasons and 19 (63%) cited failure of the experiment (usually due to plants dying, or a mistiming of the flowering period between the strawberry and borage plant). (See supplementary data S5 for locations of citizen scientists remaining engaged throughout the project).

Discussion

Companion planting is a traditional gardening practice, designed to improve crop yield by attracting pollinators and other beneficial insects. After developing a simple citizen science methodology to investigate this practice, we have shown that companion planting strawberry plants with pollinator-friendly borage increases the crop yield and the market quality of strawberry fruits.

Insect visitations

We found that the overall number of insect visitations between the test and control strawberry plants was not significantly different. However, when individual insect groups were considered, the number of visits by 'other flies' and bumblebees were more than twice as high to the test plants compared to controls, although the latter was not quite statistically significant. Borage is known to be attractive to honeybees (Garbuzov & Ratnieks, 2014; Rollings & Goulson, 2019) and bumblebees (Carreck & Williams, 2002). Here we found borage to attract a range of insects, especially bumblebees, honeybees, 'other flies', and hoverflies. This could have a positive impact on fruit set, as insect communities with diverse functional traits promote effective pollination (Woodcock et al., 2019). We conclude that, at least for 'other flies' and perhaps for bumblebees, this results in spill over to the adjacent strawberry plant. Similarly, Feltham et al. (2015) found that planting wildflower mixes adjacent to commercial strawberry crops increased insect visitation to the crop by 25%, the majority of visits being by bumblebees.

'Other flies' were frequent visitors to strawberry (similar to Ellis, Feltham, Park, Hanley, & Goulson, 2017), as well as beetles and hoverflies. Bees and flies have different foraging behaviours; bees forage and transport pollen and nectar back to their nests, whereas other insects forage only for their own needs (Ssymank, Kearns, Pape, & Thompson, 2008). These

Table 2. Fruit measurements of strawberry fruit produced by test strawberry plants paired with borage, compared with unpaired control

Measurement	X^2	df	P	Control		Test	
				Mean	SE (\pm)	Mean	SE (\pm)
Diameter (mm)	5e-04	1	0.983	23.1	0.073	23.1	0.064
Length (mm)	0.324	1	0.569	24.7	0.071	24.4	0.065
Fresh weight (g)	0.104	1	0.747	6.64	0.097	6.54	0.087
Brix ($^{\circ}$ Bx)	0.954	1	0.329	8.33	0.054	7.91	0.054
Fertilised achenes (prop)	0.457	1	0.499	0.67	0.016	0.69	0.134
Water content (g)	0.072	1	0.788	6.43	0.094	6.33	0.084

behavioural differences, together with the lack of dense hair on a fly's body, mean they aren't as effective as bees in pollinating some plant species but due to their abundance, their role in crop pollination should not be undervalued. Although flies are commonly neglected from pollination studies, they are known to pollinate over 100 cultivated crops (Ssymank et al., 2008), and are considered important contributors to global crop pollination, especially considering declines in bee populations (Orford, Vaughan, & Memmott, 2015; Rader et al., 2016). Previous studies have concluded that, in terms of strawberry crop pollination, flies provide a unique contribution, in that they visit flowers during periods of inclement weather when other pollinators were absent (Ellis et al., 2017), and hoverflies have been found to be efficient pollinators of strawberry (Hodgkiss, Brown, & Fountain, 2018). Indeed, studies conclude that it is abundance and functional trait, more than pollinator type, which contributes most to pollination efficiency in strawberries (Connelly, Poveda, & Loeb, 2015; Ellis et al., 2017). In both the citizen science and researcher experiments, beetles were also frequent visitors to strawberry plants. However, we noted in the researcher-led experiment that this was due to a high number of small pollen beetles covering the emerging strawberry flower and remaining for long periods. Previous studies suggest that Coleoptera have limited potential as pollinators of strawberry and are primarily pollen consumers (Albano, Salvado, Borges, & Mexia, 2009).

Strawberry yield and quality

Strawberry plants placed directly adjacent to borage plants produced on average 35% more fruits and 32% increased yield by weight, when compared to plants placed a distance of three metres away, suggesting the control strawberries experienced a pollination deficit in the absence of the borage plant. In addition to increasing yield, we found that companion planting with borage also improved the aesthetic quality of the fruit, with more 'EXTRA' and 'Class I' strawberries produced by the test plants. This increase in quality suggests that, due to the presence of a companion plant, more complete pollination of the achenes has resulted in aesthetically better fruit. Considering this result, it is perhaps surprising that the proportion of fertilised achenes was not significantly different between the test and control strawberry; aesthetically improved fruit may instead be a result of the even distribution of pollen. Indeed, Wietzke et al. (2018) state that an even distribution of pollen over the stigmas of the strawberry flower is important for fruit development, combined with a minimal threshold of pollen needed per stigma and, importantly, malformation may occur when these criteria are not met. It is widely agreed that bees are efficient pollinators of strawberry (Bigey, Vaissière, Morison, & Longuessa, 2005; Klatt, Burmeister, Westphal, Tscharnke, & von Fragstein, 2013; Foulis & Goulson, 2014; Klatt et al., 2014a; Feltham et al., 2015; Yanagi, Miura, Isobe, Okuda, & Yoshida, 2017; Wietzke et al., 2018; Abrol et al., 2019) often walking around the flower distributing pollen. Additionally, strawberries pollinated by bumblebees have been found to produce more marketable and better-shaped fruit (Dimou, Taraza, Thrasyvoulou, & Vasilakakis, 2008).

Future research

Consumers prefer a cosmetically perfect fruit, with recent estimates suggesting over a third of total farm production is lost due to aesthetics (Porter, Reay, Bomberg, & Higgins, 2018). Many commercial soft fruit farms buy bumblebee nests or rent honeybee hives for pollination, although the planting of strips of borage could provide an alternative, perhaps cheaper, means of boosting yields, and reducing food waste. However, this experiment was limited to individual pots in gardens and allotments: investigating whether this could work on a commercial scale under real agronomic conditions, is an essential next step. It may be that any benefits accrued from improved pollination may not offset the cost, time, and space required for the companion plants. Planting pollinator-friendly wildflower mixes adjacent to commercial strawberries has been found to increase crop visitation by bumblebees (Feltham et al., 2015), while Hodgkiss et al. (2019) concluded that intercropping strawberries with coriander, field forget-me-not, and corn mint in a commercial setting had limited benefits, with no difference in the number of marketable fruits produced.

Strawberry and borage plants in this experiment were grown in separate pots, removing any competition or interaction between the roots of the plants. In the U.K., strawberries are grown in either open ground or raised bed systems (DAERA, 2020). The current approach is therefore analogous for raised bed systems as pots containing borage could be placed alongside raised beds. However, considerations would be necessary to adjust this experiment for open ground systems, accounting for root interactions and considering space taken up by borage plants. Additionally, the seeds of borage self-sow (Sarah Raven, 2018) which would require management in open ground systems.

In our experiments, test and control plants were just 3 m apart, suggesting that the companion plant effect may be localised. The number of strawberry flowers in a commercial setting would be greater than those seen during this experiment. Therefore, the optimal arrangement and ratio of pollinator-friendly borage to strawberry plants would need consideration in a commercial setting, due to complex interactions between the density and spatial arrangement of conspicuous flowering species and pollinator response (Seifan, Hoch, Hanoteaux, & Tielbörger, 2014).

Citizen scientists

We have successfully developed a method to assess the effectiveness of companion planting, with valuable contributions from volunteer citizen scientists across the U.K. Results and patterns were consistent across data collected by researchers and those collected by citizen scientists. The engagement rate of the citizen scientists in this experimental project was good, with 27% submitting data forms and 55% continued engagement, compared to a report stating an average of 27% participants return to a project for a second time (Sauermaun & Franzoni, 2015). Therefore, this experimental citizen science method could be adapted for other companion plant combinations, all the while engaging the public in wildlife gardening. Future pollination-based experiments should incorporate sessions of

remote training to increase the accuracy of insect identification (Ratnieks et al., 2016).

Acknowledgements

I would like to thank all the ‘*Super Strawberries*’ citizen scientists whose hard work contributed to this project, and to the campus-based volunteers involved in counting, measuring and watering: Charlotte Cook, Emma Eatough, Janette Rogers, Connor Sullivan. Thank you to Rachel Nichols for statistical help using R. PhD funding for this project was provided by C.B. Dennis British Beekeepers’ Research Trust and The University of Sussex. The authors report no conflicts of interest.

Author contributions

J. Griffiths-Lee, E. Nicholls and D. Goulson conceived the ideas and designed methodology; J. Griffiths-Lee collected and analysed the data, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Postcode locations of all citizen scientists enrolled in project, highlighted on a map of the U.K.

Data S2. Citizen science workbook. Printed workbook as part of the project pack sent to volunteers, containing sheets to record insect visitations and strawberry harvest.

Data S3. Citizen science instructions. Printed instructions as part of the project pack, detailing instructions on plant care, project set up and data collection.

Data S4. Citizen science pollinator ID guide. Printed ID guide as part of the project pack, a simple guide to the identification of different insect groups.

Data S5. Postcode locations of citizen scientists remaining engaged throughout project, highlighted on a map of the U.K.

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Accepted 13 April 2020

Associate Editor: Adam Vanbergen